

On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees

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Abstract

The following question is posed and discussed. Under what environmental conditions will the action of natural enemies prevent competitive exclusion between species of their prey? My studies on marine animal populations and rain forest trees both suggest that fluctuations in the physical environment and subsequent effects on the supply of resources reduce the effectiveness of natural enemies and allow the prey to increase to sufficiently high densities that they compete for resources. Fluctuations in weather may (1) reduce the populations of enemies more than their prey, (2) allow the prey to get a head start after an unfavourable season and (3) reduce the degree of specialization of the enemies. With lesser amplitude and/or more regularity of fluctuations, natural enemies are more effective in preventing competition. However, these conditions also lead to stronger defenses by the prey and greater effectiveness of the secondary enemies attacking the ones in question. In regions of very favorable physical conditions, the only defense against natural enemies seems to be rarity and widely scattered distributions, which together preclude competitive exclusion.

Interspecific competition is defined as the striving by members of two or more species, at the same trophic level, for the same requisite which is in short supply. It is often invoked to explain the organization of ecological communities, the evolution of closely related species, character displacement where ranges overlap, etc. While competitive interactions may be observed on occasion, the competitive exculsion or displacement of one species by another from a local area has seldom been documented clearly, as pointed out by Miller (1967). It is usually suggested that the reason why competitive exclusion is rarely seen is that in the past, competitors have evolved divergent strategies to share the contested resource. However, in many ecological communities, very similar species coexist with little obvious divergence in character. They often appear to be using completely the resource required; they seem to be competing, but not excluding each other.

An alternative hypothesis to explain such coexistence is that potentially competing prey populations are kept at such low numbers by very efficient predators that competition is greatly reduced. The prey coexist because no species reaches high enough density to exclude another in competition. There have been several experimental tests of this hypothesis, both in artificial populations such as crops, heavily grazed pastures or in the laboratory, and under more natural conditions. Probably the first experimental test of this idea was performed by Charles Darwin (1859, p. 67-68): 'If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous, though fully grown plants; thus out of twenty species growing on a little plot of mown turf (three feet by four) nine species

perished, from the other species being allowed to grow up freely.'

Harper (1970) has reviewed and discussed later experiments in which herbivores were removed from or added to highly modified vegetation, such as grazed pastures, sown swards and stands of introduced plant pests such as prickly pear or St. John's wort. The intensity and timing of grazing and the selection of prey had profound effects on the composition of the vegetation. In all these studies the implication was that grazing reduced the populations of certain species, allowing others to persist or enter.

In the laboratory, Slobodkin (1964) showed that when *Hydra* and *Chlorohydra* were kept in the light, *Hydra* became extinct. He then imposed 'predation' by removing a fixed percentage of both species. As the percentage of predation increased, so did the time to extinction of *Hydra*, until at 90% predation the two species were coexisting when the experiment was ended.

Under more natural conditions, removal of enemies has sometimes resulted in changes which are attributed to increased competition. Examples are the removal of rabbits from herbaceous stands in Britain (Harper, 1970), small mammals from herbaceous vegetation in young plantations of trees (Summerhayes, 1941) and marine grazers or predators from rocky shores (Connell, 1961b; Paine, 1966; Paine and Vadas, 1969).

In summary, it seems clear from these experimental manipulations in the laboratory, in simplified field situations such as crops and pastures, and in natural communities, that enemies can prevent competition between some of their prey species. The question is: Under what conditions will this happen in natural ecological communities? Since the most convincing case for the existence of 'organization' in an ecological community is the operation of interactions such as competition and predation, it is important to try to define the conditions that determine how and when these interactions operate effectively under natural conditions.

In the following case histories, I will provide some evidence concerning the conditions which determine whether predation will or will not be effective in preventing competition. These studies were made in largely undisturbed natural communities in which the species had their full complement of competitors, predators, parasites and food species.

Predation ineffective in preventing interspecific competition in intertidal barnacles

In a study of interspecific competition and predation in Scotland, I found that one species of barnacle excluded another species from most of the intertidal shore (Connell, 1961b). The losing species, *Chthamalus stellatus*, settled normally only in the upper half of the intertidal zone, and was displaced from it by direct crowding during growth of the winning species, *Balanus balanoides*. In this upper shore region, the predatory snail *Thais lapillus* attacked mainly *Balanus* but did so only after the prey were at least 6 months old (Connell, 1961a). By this time, much of the competition between the barnacles had already occurred, so that the predation could not lessen the competitive exclusion of *Chthamalus* by *Balanus*. At lower shore levels, *Thais* began to attack the barnacles when they were only about a month old. When I transplanted the competing barnacles to these lower shore levels, the predation was more effective in preventing competition. At each monthly census I made notes of which *Chthamalus* were being crowded by *Balanus*. Table 1 shows the mortality of *Chthamalus* caused by this crowding. Mortality from crowding was about the same at both levels when predators were excluded by cages, but in natural populations the predators reduced this crowding only at lower shore levels.

Table 1. The amount of mortality due solely to crowding in natural populations of *Chthamalus*, open to predation by *Thais* and protected from predation in adjacent cages. *Chthamalus stellatus* was competing with *Balanus balanoides*, the predator being *Thais lapillus*, at Millport, Scotland, 1954 (Connell, 1961b). *Chthamalus dalli* was competing with *Balanus glandula* and *B. cariosus*, the predators being *Thais emarginata* and *T. lamellosa* at Friday Harbor, Washington, USA, 1964.

	<i>Chthamalus stellatus</i>				<i>Chthamalus dalli</i>			
	upper shore		lower shore ¹		upper shore		lower shore	
	open	cage	open	cage	open	cage	open	cage
Number of sites	2	2	3	3	2	3	6	6
Number of <i>Chthamalus</i> in June	98	153	118	152	232	493	468	593
% mortality of <i>Chthamalus</i> by September, due to crowding by <i>Balanus</i>	31	39	13	32	6	22	10	37

¹ These barnacles were on pieces of rock from the upper shore, transplanted to the lower shore.

The question then is: Why weren't the predators so effective at upper shore levels? Why didn't they begin to attack the very young barnacles as they did at the lower levels? To answer these questions, I will describe another example, from a similar community in which the predators did this.

Predation effective in preventing interspecific competition in intertidal barnacles

On San Juan Island, Washington, USA, 3 species of barnacles live in the intertidal zone with 3 species of their principal predators, snails of the genus *Thais* (Connell, 1970). The vertical distribution of the two species of *Balanus* on San Juan Island is virtually identical with that at Millport, Scotland; adults of *B. glandula* were confined to a narrow band at the top of the intertidal zone, similar to *Chthamalus* at Millport. *B. cariosus* occupies the lower zone, like *B. balanoides* at Millport. But the reason why *B. glandula* only survived high on the shore on San Juan Island was not because it was excluded from the lower shore by competition with *B. cariosus* or any other competitor. Every year *glandula* settled throughout the lower shore but was quickly eaten by predators. The predators could not feed at the highest shore levels where adult *glandula* survived for several years. In situations where predators were absent, *glandula* survived throughout the intertidal zone. One such habitat was at the head of quiet bays, where both predators and other barnacles were rare (Connell, 1970).

In situations with at least moderate water movement, predators were common and fed heavily on both species of *Balanus* when the barnacles were young. With this intense predation the barnacles were seldom allowed to get dense enough to compete for space; I have seen crowding in *B. cariosus* occasionally, but never in *B. glandula*, or between the species. I several times attempted to exclude *Thais* with cages, as I did in Millport, but small *Thais* invariably got inside cages and attacked *B. glandula* preferentially. I have never managed to exclude predators for long enough to see which species of *Balanus* would win in competition. Since *cariosus* grows slightly faster than *glandula*, I would predict that *cariosus* would win.

Occasionally, a heavy settlement of *Balanus cariosus* survives at high shore levels, possibly because of unusually favorable cool weather during the settlement season. These

may then crowd out the other species of barnacles because predation is much less intense at very high levels. This evidently happened to the 1963 settlement at the study area at San Juan Island. When this species reaches the age of 2 years, it becomes invulnerable to attack by *Thais* in the intertidal zone, and so survives a long time. Since this only happens occasionally, the age structure of the *B. cariosus* population consists of one or more 'dominant year classes', rather than the more evenly mixed age distribution of *B. glandula*.

Another species of barnacle, *Chthamalus dalli*, occurs scattered throughout the intertidal zone and not restricted to any particular level. In its small size and slow growth it resembles *C. stellatus* at Millport. I set up a series of cages to test the outcome of competition between *C. dalli* and the two species of *Balanus*, in the absence of predation. At each monthly census I made notes of which *Chthamalus* were being smothered, undercut or crushed by adjacent *Balanus*. Table 1 shows the mortality from this competition for the first summer when growth was most rapid. At both shore levels, mortality from crowding was much higher inside the cages. The predators outside were eating the *Balanus* and thus reducing the competition, as they did on the transplanted rocks at lower shore levels at Millport. But on San Juan Island, the predators were effective at almost all shore levels in keeping the barnacle populations below the point where they would compete for space. Only occasionally at very high levels did *B. cariosus* escape predation long enough to become dense and crowd out other competitors. Above this, in the narrow high band where adult *B. glandula* survived in a refuge above its predators, the barnacle population seldom occupied all the space (Connell, 1970, Fig. 8). Probably the harsh physical conditions at this high level kept the population sparse, as happened at Millport (Connell, 1961, Table 13).

The predator responsible for most of the predation at upper shore levels was *Thais emarginata*. It has a relatively thinner shell, larger opercular opening and shorter spire than either *Thais lamellosa*, which lives at low levels on San Juan Island, or *Thais lapillus* from Millport. As Kitching, Muntz and Ebling (1966) and Connell (1970, Table 17) have shown, the shell characteristics of the latter two species protect them from predation by shore crabs which feed at low shore levels. Evidently *Thais emarginata* has a refuge from crab predation at the higher shore levels, and does not require a heavy shell. Since it is reasonable to assume that constructing and carrying a thinner shell requires a lesser expenditure of energy, this saving may compensate for the disadvantages both of taking smaller sized prey and of having a shorter feeding period at high levels. Compared with *Thais lamellosa* from lower shore levels, *Thais emarginata* is smaller, has a thinner shell, reaches sexual maturity faster ($1\frac{1}{2}$ years as against $2\frac{1}{2}$ years for *T. lamellosa*) and lives a shorter time (3 to 4 years as against 8 or more years for *T. lamellosa*).

This specialized strategy has a price; *Thais emarginata* cannot retreat to lower shore levels if its food supply fails, because its shell structure renders it very vulnerable to predation by crabs. Therefore, it is dependent upon a very regular food supply. On San Juan Island *B. glandula* fulfills this requirement nicely; its recruitment is very regular (Connell, 1970, Fig. 4). Thus the prevention of competition at upper shore levels at San Juan Island is probably due to the presence of a specialized predator which harvests its prey very efficiently. The specialization is permitted by the existence of a dependable food supply, *B. glandula*.

In contrast, there is no such specialist predator at Millport, probably because the food supply is much more variable there. *B. balanoides* often reaches densities of 60 to 80 per cm², but in some years the settlement fails almost completely (Connell, 1961a). A high

level specialist like *Thais emarginata* would occasionally starve in Millport. Apparently, the reason for the irregular barnacle recruitment in Scotland is due to the very short season of larval settlement. The population of *B. balanoides* liberates its larvae in two successive waves within one to one and a half months in early spring, in response to the phytoplankton bloom (Barnes, 1957). In some years, the first liberation perishes when the early bloom fails due to weather conditions. Occasionally both liberations perish and settlement is almost non-existent (Barnes, 1956; Connell, 1961a).

In contrast, the larval settlement of *B. glandula* on the Pacific Coast extends over six months. It is much less likely that weather catastrophes could completely eliminate the larval supply if settlement extends over six months, than if it occurs over a short period as in Scotland. As a consequence, recruitment of *B. glandula* was very regular.

Thus, the predator-prey system in Scotland is geared to a highly seasonal, rather un dependable resource supply. There is a short intense spring bloom of phytoplankton, which demands close synchrony of liberation of the barnacle larvae, and there are occasional failures due to weather catastrophes. This system limits the degree of specialization of the predators, and decreases their efficiency in harvesting their prey in certain habitats. With less efficient predation and short intense recruitment of prey, strong competition develops between the prey species.

At San Juan Island, less seasonality in primary productivity probably allows a longer period over which larvae can be released into the plankton. This reduces the uncertainty of recruitment of prey to the shore population and permits specialization of the predator. It can keep up with the prey, thinning it out and preventing competition for space, as the predator *Pisaster* did in Paine's (1966) study.

On the prevention of competitive exclusion in rain forest trees

In contrast to the barnacles which were kept by their predators below the maximum level allowed by the resources available, trees in rain forests obviously compete for light and possibly for other resources. Their natural enemies, as a group, don't prevent competition between the trees. However, the enemies may prevent competitive exclusion of one species of tree by another, by preventing any one from forming a single-species aggregation and so displacing other species from the particular area.

The mechanism I suggest is that each tree species has host-specific enemies which attack it and any of its offspring which are close to the parent. The healthy parent tree supports a large population of these enemies without itself being killed, but the seedlings, whose growth is suppressed in the heavy shade, succumb to the attack of insects and other enemies which come from the parent tree itself or the soil below it. A similar hypothesis, though differing in certain details, has been proposed independently by Janzen (1970).

So the only way a species of tree can reproduce in these forests is to disperse its seedlings far enough from the parent to allow them to escape attack for long enough to reach the size when they can withstand attack by enemies. If all enemies of trees were removed from an entire forest, each species would probably form small groves, and the more rapidly growing species would gradually spread over the habitat it is best suited for, excluding the slower growing or less well adapted species in that area. The final result would be a lower 'pattern' diversity (less intermingling of the different species) and as a consequence, fewer species in any local area of forest.

The following is a preliminary account of work which I have done with J. G. Tracey and

L. J. Webb in rain forests in Queensland, Australia, in an effort to test this hypothesis (Connell, Tracey and Webb, in prep.). We mapped the trees in two rain forests, the larger ones (> 10 cm in diameter at breast height (DBH)) on areas of about 1.7 hectares, the smaller ones in strips within these plots.

Table 2 illustrates how the diversity increases with size and age of trees in the plot in northern Queensland. Seedlings up to 0.1 m high (less than about 4 years old) had a very low 'pattern diversity' (Pielou, 1966); that is, they tended to occur in single-species clumps rather than mingled with other species. (This sampling was done by taking the first and second nearest neighbours of each individual and recording the number of species in the 'triplets'.) In young trees of the next larger size class, 0.11 to 0.19 m high, the pattern diversity increased markedly, and by the time they were over 0.8 m high, their pattern diversity had approached that of the adult trees. Pielou's index of pattern diversity takes into account the number of species and their relative abundance. We have given reasons (Connell, Tracey and Webb, in prep.) why a high pattern diversity should lead to a greater species diversity and 'evenness' as shown in Table 2.

Table 2. Diversity of trees in rain forest at Davies Creek, North Queensland, Australia, lat. 17° S, elevation 850 m. Saplings less than 2.5 cm in diameter (breast height) were divided into five height classes as equal in number as possible. All the data refer to August, 1969, except those in the second column from the right, and for trees larger than 2.5 cm in diameter. Pattern diversity was calculated as shown in Pielou (1966): for trees 0.11 to 6.34 m high, the 1969 figures are from the same group of trees as in 1965, minus those which died in the interval.

Height class (m)	Number of trees	Number of species	Diversity H (base e)	Evenness J	Pattern diversity D	
					Aug. 65	Aug. 69
0 -0.10	1080	71	2.05	0.39	—	0.51
0.11-0.19	1038	115	3.47	0.66	0.72	0.77
0.20-0.35	983	103	3.38	0.64	0.76	0.82
0.36-0.79	1040	111	3.60	0.68	0.87	0.89
0.80-6.34	1093	131	3.80	0.72	0.93	0.93
Diameter						
class (cm)						
2.5-9.9	956	116	3.79	0.72	0.96	—
10.0 +	1502	126	4.31	0.81	0.98	—

The pattern diversity increases not only with size but also with age, as shown in Table 2 by the changes between 1965 and 1969. The increase in pattern diversity was greater in the smaller size classes where mortality was greater. This suggests that mortality falls more heavily on trees which are next to others of the same species, than on those intermingled with other species. Since we had mapped every individual in 1965, we could test this hypothesis by tabulating for each tree whether its nearest neighbour was the same or a different species. As shown in Table 3, the small saplings having the same species as a nearest neighbour had a higher mortality rate than if they had a different species as neighbour. Larger saplings had a lower mortality and the species of the neighbour had no effect.

Adult trees also have a deleterious effect on smaller trees of the same species. We planted

Table 3. Mortality of tree saplings in rain forest in relation to the species of their nearest neighbour within the same size class. August 1965 to August 1969, Davies Creek, North Queensland, Australia, lat. 17° S, elevation 850 m.

Height class (m)		Species of nearest neighbour	
		same species	different species
0.11–0.19	Number living in 1965	64	148
	Number dying by 1969	24	27
	% mortality in 4 years	37.5	18.2
0.20–0.35	Number living in 1965	153	435
	Number dying by 1969	33	49
	% mortality in 4 years	21.6	11.2
0.36–0.79	Number living in 1965	100	548
	Number dying by 1969	11	36
	% mortality in 4 years	11.0	6.6
0.80–6.34	Number living in 1965	59	604
	Number dying by 1969	2	18
	% mortality in 4 years	3.4	3.0

seeds of *Planchonella sp. nov.* in four plots of 2 × 1 m each under two adjacent adult trees, and in four other plots nearby under adult trees of other species. In each place we cut the roots around 2 of the plots to eliminate competition for nutrients with the adult trees. Over 80% of the seedlings became established in all plots. The results in Table 4 indicate that mortality of the young trees during the next 3 years was much greater under adults of the same species than under those of other species. Removal of roots had no consistent effect; it certainly did not improve the survival under adults of the same species.

In other experiments we placed the seeds of other species on the surface instead of burying them, both under adults of the same species and of different species; some were protected by cages of 1 cm mesh chicken wire. To test the effect of density, we placed seeds one meter apart in a line through the forest as a 'sparse' treatment for comparison with the 'dense' treatments described above where the seeds were 100 per m². An insecticide spraying treatment wasn't effective; indications of insect attacks were as prevalent in

Table 4. Mortality between 2 February 1967 and 4 April 1970 of seedlings of *Planchonella sp. nov.* at Davies Creek, North Queensland, Australia, lat. 17°S, elevation 850 m. Seeds were planted under mature trees of the same species and under trees of other species. Each of the eight plots was 2 × 1 m and contained 98 seeds. Half of the plots were trenched, all roots being cut to a depth of 0.3 m.

	Number dying out of 98			
	under adults of the same species		under adults of a different species	
	plot 1	plot 2	plot 1	plot 2
Trenched	65	69	14	26
Not trenched	50	54	25	42

these plots as in the other treatments. Seeds of *Cryptocarya corrugata*, from the plot itself, and *Eugenia brachyandra*, brought from the other plot at 27° S, were used. None was used if it had already been attacked by insects. As shown in Table 5, almost every seed was killed within a year, regardless of its position or density. Since seeds were killed inside cages and since many seeds had holes caused by insect attack, it is probable that insects were the main cause of death. For these species, at least, the increase in pattern diversity evidently occurs after germination, not in the seed stage. That is, all seeds are probably killed most of the time, but in occasional years a seed crop may escape when, for some reason, the seed eaters are reduced. Then a great number of new seedlings becomes established in a patch, and these are attacked and thinned out over the succeeding years. The fact that both the evenness component of diversity and the pattern diversity were very low in the young trees which entered the population between 1965 and 1969 (Table 2, height class 0 to 0.1 m), is evidence that recruitment followed this pattern on the study site. This model differs from that proposed by Janzen (1970). He suggests that the probability of a fallen seed surviving is a function either of its distance from the parent or its population density. In the species I studied, neither was related to survival. However, we agree on the fundamental point that overall survival should be greater at greater distances from the parent. My data indicate that the mortality which increases pattern diversity occurs mainly after germination during the seedling and sapling stages.

Evidently, mortality is greater when individuals of the same species grow together than when they are intermingled with other species. At least three possible mechanisms could produce this effect. Firstly, each species might secrete toxins into the environment which poison individuals of its own species more than those of different species. Although this

Table 5. Survival of seeds of two species of rainforest trees, placed on the surface of the ground at the Davies Creek plot, North Queensland, 17°S. lat., 850 m. Seeds of *Cryptocarya corrugata* were from this plot. *Eugenia brachyandra* seeds were from South Queensland, 27°S. lat., 850 m. The figures are numbers of seeds at the start of the experiment in September, 1969, and of germinated seedlings in June, 1970.

	Under adults of same species		Under adults of other species	
	Sep. 69	June 70	Sep. 69	June 70
<i>C. corrugata</i> , 'dense', 100/m ²				
Control, no treatment	134	1	130	0
Under wire mesh roof	75	0	75	0
Inside wire mesh cage	75	0	75	0
Insecticide, 0.1 % Dieldrin	141	0	129	2
	Sep. 69	June 70		
<i>C. corrugata</i>				
'sparse', one seed every meter in a line through the forest	100	0		
<i>Eugenia brachyandra</i>				
'dense', 100/m ²	100	0		
'sparse', one every meter in a line through the forest	100	1		

remains a possibility, it seems less likely than the others. The second possibility is that each species has such specialized requirements for nutrients that competition is more severe between plants of the same species than with plants of different species. However, the results of the experiment in Table 4 seem to exclude the possibility that intraspecies root competition with adults was more deleterious than interspecies competition. Competition between adults and young trees in these dense rain forests is probably primarily for light, not for soil nutrients or water. Competition for light should not be more severe within than between species, unless different species produce qualitatively different sorts of shade. On the basis of present evidence this mechanism seems less likely than the following one.

The third possibility is that attack by natural enemies is heaviest when trees live in single-species aggregations, rather than mixed with other species. There has been, to my knowledge, no direct experimental test of this hypothesis, but there is much indirect evidence (Gillett, 1962). For example, single-species stands such as rubber plantations were unsuccessful in their native Brazil where they were heavily attacked by disease. But, when introduced into Asia without their native enemies, they could be grown in plantations. In our own work (Table 4) there was much more grazing on the seedlings planted under adults of the same species than on those under other species.

For this mechanism to be effective the enemies must be both specialized in their choice of prey and not particularly mobile. Populations of insects or fungi centering their attention on an adult tree would probably be the most effective at producing the high pattern diversity we observed. Obviously, other factors, particularly heterogeneity in space and time, provide other opportunities for the maintenance of diversity in rain forest trees. I suggest that the role of predation is important in preventing trees from forming single-species groves, which is probably the only way in which one species of tree could exclude others by interspecies competition.

Conditions determining the effectiveness of natural enemies in preventing competitive exclusion in their prey

What circumstances determine whether natural enemies can prevent competitive exclusion between prey species? From the examples discussed above and from the studies of other workers, it seems clear that fluctuations in the physical environment decrease the effectiveness of natural enemies in several ways.

Firstly, prey populations are apparently less vulnerable to the direct effect of extreme fluctuations in weather, than are their enemies. For example, Michelbacher and Leighy (1940), Lord and MacPhee (1953) and DeBach, Fisher and Landi (1955) all found that extremes of weather killed a much higher proportion of the natural enemies than of their prey, herbivorous insects. Why this should be so isn't known, although it is probable that the enemy would be more exposed to the effects of weather when it was searching than would its prey, sheltered by the vegetation. However, this is not the whole story since much of the mortality occurred during winter when the parasite was a larva inside the hibernating host (Lord and MacPhee, 1953). On the intertidal shore, barnacles extend higher than their predators, evidently being better able to withstand the extremes of weather at the very high levels.

Secondly, fluctuations of the weather can reduce the effectiveness of natural enemies in less direct ways. After the reduction in numbers or activity of both predator and prey during an unfavorable season, the prey populations may recover and grow quickly to

densities at which they begin to compete with each other before the predator populations have increased enough to control them. This evidently happens at high latitudes where phytoplankton blooms or huge swarms of insects occur in the spring. The favorable season may be so short that the natural enemies don't have time to increase enough to control their prey. In this respect the terrestrial high arctic resembles the high intertidal zone where there is too short a time for the predators to feed effectively. At the lower edge of the intertidal zone, the predators can feed almost continuously, as they can in those parts of the terrestrial wet tropics with little seasonal change. Even though the natural enemies have evolved to respond rapidly to such spring increases in their prey – as for example the release of barnacle larvae in response to an increase in phytoplankton, or the spring migration of insectivorous birds into the arctic – the prey may still outstrip them for a while.

Thirdly, irregular or unpredictable fluctuations in the physical environment may cause such unpredictable variations in the supply of some critical resource, such as the numbers of a species of prey, that the natural enemy cannot afford to specialize on it. This is probably the reason why *Thais lapillus* has not specialized to the extent that *Thais emarginata* has, with the consequence that *T. lapillus* cannot attack the barnacles on the upper shore early enough to prevent competition. Whether specialist predators are usually more effective in reducing their prey than generalists is hard to say at this time. In Paine's (1966) example, the large predatory starfish, *Pisaster ochraceus*, kept the mussel populations from competitively excluding other species. *Pisaster* is specialized in feeding if given several species of prey in equal abundance, showing a preference for mussels (Landenberger, 1968). Thus one would predict that when *Pisaster* first moved into a new area mussels would be common, and it would feed as a specialist on them, reducing their competitive effect. Thereafter, as shown by Paine (1966), it would feed more generally on a greater variety of the species of sedentary animals available. Thus when *Pisaster* was reducing the dominant prey it was acting as a specialist.

Other independent evidence that specialists are more effective than generalists in reducing their prey is, unfortunately, lacking. Although it is often stated (DeBach et al., 1964) that the best biological control of pests is done by highly specialized enemies, there has never, to my knowledge, been a test of this idea. Specialists are used in biological control, not because they are known from independent evidence to be more effective than generalists, but because they are not likely to attack beneficial plants or animals after they are introduced to a new country.

Another example of differences in degree of specialization is the common observation that species nearer the 'top' of food webs tend to be less specialized in their choice of food. For example, Paine (1963, 1966) has found that whereas small predatory snails in the rocky intertidal habitat eat only a few species of suspension feeding or herbivorous grazing animals, the larger snails and starfish eat more species, including both the smaller predatory snails and their prey. Brues (1946) points out that herbivorous insects often feed on only one or a few species of plants, whereas many predatory insects attack many species of herbivorous insects. Also, he states that entomophagous parasitoid insects usually have fewer species of hosts than the hyperparasites, which often attack both the herbivorous host and the entomophagous parasitoid. If, as discussed earlier, unfavorable weather causes less fluctuation of populations at lower than at higher trophic levels, this would permit greater specialization of animals feeding on organisms at lower levels. Thus for several reasons, one might expect greater specialization and presumably greater effectiveness of natural enemies at lower trophic levels.

In summary, in the sort of environment with fewer irregular occurrences of extreme weather, and lower amplitude of variations in temperature, rainfall, etc., natural enemies will be most effective in preventing competitive exclusion in their prey. In such places the enemies should be more specialized, especially at lower trophic levels. There will be less chance for the prey to increase suddenly until it is beyond control of the predator, since the unfavorable seasons will be reduced in length and severity.

However, these same environmental advantages also work to diminish the effectiveness of natural enemies in at least two ways. Firstly, there will be strong selection on the prey to evolve defences which not only protect them from existing enemies, but also have the effect of reducing the number of species attacking them. Defences of the prey, for example plants with poisonous chemical substances or spines, or animals with armor, protective coloration, etc., require specialized methods of attack by the predator. Such a requirement for specialization must reduce the number of species of predator which can attack a particular species of prey. With fewer species of natural enemies there is a greater chance of the prey escaping. There is evidence for this from work in biological control; a pest of the olive, which was somewhat reduced during the cooler seasons by one species of enemy, was almost eliminated when another enemy species was introduced which attacked it in the summer (Huffaker and Kennett, 1966). Holling (1959) indicated that control of the European pine sawfly in Canada was more likely with several species of mammalian predators, each of which was most effective at a different prey density.

Secondly, such favorable environments also increase the effectiveness of the species of predators or parasites which attack the natural enemies in question. Since even large carnivores have parasites, and general predators feed on hyperparasites, no species is without its complement of natural enemies. For this reason, as natural enemies become more effective in more favourable climates, it becomes more difficult to predict whether, for example, plants will be reduced more significantly by herbivores than the herbivores by their predators or parasites. In some instances, such as in the rain forests I have studied, herbivores seem to be reducing competitive exclusion of the plants. But in the second growth of dry savannah woodlands in Central America, ants living on swollen-thorn *Acacia* trees kill both the herbivorous insects and the nearby competing vegetation (Janzen, 1966). In any event, in places with a more predictable or less fluctuating physical environment, attacks by natural enemies at all trophic levels would be expected to be more intense and continuous. The great increase in incidence and intensity of parasitism in humans as one approaches the equator is probably the best available evidence of this trend (LaPage, 1963).

In contrast, in areas with extreme and irregular fluctuation in climate the prey often escape their natural enemies and reach densities at which they compete for resources. As the amplitude and irregularity are reduced, natural enemies become more effective. In a completely constant benign physical environment, natural enemies should be very specialized and effective in finding almost all prey. In this situation, the only way in which any species could exist would be to be so rare and widely scattered that some individuals escape being found by their specialized natural enemies, at least until they are well established and reproductively mature. Because no environment is constantly benign, no ecological community is so organized. However, as one approaches such conditions in a tropical rain forest or coral reef, species certainly do become scarcer and more widely scattered amongst individuals of other species. I believe that increased effectiveness of natural enemies accounts for this trend.

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Discussion

Participants: Connell (Author), den Boer (P. J.), Cavers, Clough, Jacobs, Jain, Kuenen, Murdoch, Pimentel, Rosenzweig, Solomon, Turnock and Watt

This work seems to be in keeping with a generalization, that in ecosystems which have evolved in stable environments for a long time, species maintenance is more by subtle behavioral or biochemical mechanisms than is the case in immature north and south temperate zone ecosystems in unpredictable environments. The fact that there are a great number of poisonous fish species in shallow coral seas, whereas these are absent in e.g. the Great Lakes, which are highly unstable, may bear on this (WATT). However, many poisonous species of fungi (mushrooms) are found in the subarctic Scandinavian forests; what is the position in the tropics (CLOUGH)?

The tropic zone may well be less variable than the temperate and arctic zones, but it is not clear that it is a more predictable environment (MURDOCH). The level of differences between seasons in arctic and boreal continental regions may be highly predictable. Moreover, in connection with the variability of tropic and temperate zones the influence of natural selection may have been such that animals in some tropic regions are about equally susceptible to the rather subtle weather changes prevailing there as are animals in temperate regions to more pronounced weather changes (DEN BOER). I agree with this (AUTHOR).

If one starts with a clumped distribution (as was the case with the small rain forest trees), and then allows mortality work at random, would not the spatial pattern diversity index increase towards 1? This would seem to mean that the supposed neighbourhood (intra-specific) competition is not needed to get an increase of spatial diversity with increase of tree size (JACOBS). This could easily be simulated. But random mortality should not kill trees with nearest neighbours of the same species more than those with nearest neighbours of different species, as was shown to be the case. And if mortality is random, pattern diversity should stay the same (AUTHOR).

It shown that species diversity and pattern diversity increase with tree height classes. But what is the possible effect of patterns of diversity between different tree heights on the changes in overall diversity measures (JAIN)? The neighbours used were all within the same height class. But the two nearest neighbours which were smaller than the central individual could be used to get some idea of the influence of larger trees on the pattern of smaller ones (AUTHOR).

How do you explain there being a higher number of species in the taller group than in the lowest height class, if only random mortality is involved (JAIN)? The height classes are not age classes, and the larger classes probably represent much longer periods of time. The smallest class are offspring only of those species which reproduced successfully over the past few years (AUTHOR).

Healthy phytophagous sawfly larvae on larch trees do not drop from trees, even during

rather violent storms, unless they have completed feeding or are depleting the foliage. Therefore, it seems unlikely that small trees under large ones, which support low densities of phytophagous species will be destroyed by this means (TURNOCK). In the tropics trees might 'declare a territory' by raining insects on their surroundings, by abscission of twigs and leaves having insects on them (ROSENZWEIG).

To explain a presumed non-random mortality of seedlings under a tree of the same species it is not necessary to assume the presence of specialized feeders. Each phytophagous insect coming down from the tree overhead will find seedlings of the same species more available than those of other species; moreover, it is very probable that even extreme generalists will show some preferences. There may be another complication; in temperate regions many phytophagous insects show a definite preference for small and young trees; to give an example: whereas nearly all leaves of the available young birches may be rolled up by *Deporaus betulae* (or other *Rhynchitini*), mature trees are hardly infested. How does this compare with the tropics? (DEN BOER). The problem is the meaning of 'more available'. Several species of young trees occur under a single large tree; if they are all of about the same size, they are equally available to any phytophagous insect. If the insects eat them without preference, i.e. in the same proportion in which they occur, those of the same species as the adult tree above need not be removed proportionately faster there than under adults of a different species. To produce the results shown in Table 4, the insects must specialize to some degree on young trees of the same species as the adult. Since most insects do show some preferences, this will probably happen. In regard to the second point, a greater rate of attack on young trees would intensify the removal of seedlings; I have no data on whether this tendency also occurs in the tropics, but I expect that it does. (AUTHOR).

If something tends to prevent the growth of seedlings under a mature tree of the same species, this may be of advantage to the species, by giving preference to its seedlings a few meters away where the species has not depleted the soil of trace elements, etc., corresponding to its particular needs (SOLOMON). The experiment shown in Table 4 indicates that competition for soil nutrients between seedling and parent is not important in the species studied (AUTHOR).

There are examples of progeny arising only from the exact site of the parent plant. Koller and Roth (*Am. J. Bot.* 51, 1964) working with *Gymnarrhena* in the desert areas of Israel found that two kinds of seeds are produced (amphicarpy). One kind is light, aerial and wind dispersed. The other kind is heavy and is produced below ground; here the offspring actually grows up through the dead tissues of the parent plant. This site would be the most favourable for the species in a very unfavourable environment (CAVERS).

Is it not possible for two competitors to coexist although they are feeding on the same living resource if the food host can evolve differentially to the two competitors (PIMENTEL)? Perhaps, but this is not possible in plants whose food does not evolve. Probably it will occur in some animals, but the barnacles studied were competing for a resource which does not evolve either, namely space (AUTHOR). See also the discussion after the paper of Pimentel.

A few *Chthalamus* individuals survive and reproduce in the region of competition with *Balanus*, but they are smaller and so contain fewer larvae than uncrowded ones (AUTHOR to JAIN).

Could there be any selective pressure toward a greater heterogeneity of dispersion; compare Birch: *Cactoblastis-Opuntia* (JAIN). After a period in the plankton the offspring do not

necessarily return to the habitat of the adults. Most of the offspring come from the upper shore zone where there is no competition with *Balanus*, and where this presumed selective advantage of aggregation would be less (AUTHOR).

Studying more cases and more species, experimentally, on rocky coasts may indeed upset some of the conclusions so far reached (AUTHOR to KUENEN).